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# CELLS RESPONSIVE TO FREE-FIELD AUDITORY STIMULI IN GUINEA-PIG SUPERIOR COLLICULUS: DISTRIBUTION AND RESPONSE PROPERTIES

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SUMMARY

1. We have investigated the responses of superior colliculus neurones in the anaesthetized guinea-pig to free-field auditory stimulation.

2. The auditory cells were located throughout the deeper laminae and also in the lower part of the stratum opticum. Auditory cells were not found in the rostral pole of the superior colliculus.

3. The auditory responses consisted of a few spikes at stimulus onset with a latency from stimulus arrival at the ear of 7–27 ms. Frequency response areas were measured for forty-five neurones; many of these areas were broad or multipeaked although some were well defined and 'V' shaped. White noise was a more effective stimulus than tones.

4. The majority of cells in our sample responded best to sounds from a restricted horizontal location. Two major response types were found: (1) neurones responding to the same localized area of space despite changes in sound level and (2) neurones responding only to a localized area of space near threshold, but to an extensive area for louder sounds.

5. As the site of the recording electrode was moved from the rostral to the caudal part of the superior colliculus, the location of the auditory receptive fields shifted from the anterior to the posterior field of the animal, thus indicating the presence of a map of auditory space.

6. The visual projection to the guinea-pig superior colliculus was determined and found to be similar to that in other vertebrates.

7. Comparison of visual and auditory space maps in the guinea-pig superior colliculus reveals that receptive fields are coincident over a wide range, but severe discrepancies were evident between the visual and auditory receptive field positions represented at single locations in rostral and caudal colliculus.

## INTRODUCTION

Electrophysiological and behavioural studies indicate that the superior colliculus is concerned with the localization of novel stimuli and with the control of orienting movements of eyes, head and body (see for example Gordon, 1975; Sprague, Berlucchi & Rizzolatti, 1973; and Wurtz & Albano, 1980 for detailed reviews and references).

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This laminated structure can be subdivided into two major functional parts: the superficial layers 1–3 which receive visual inputs and the deeper layers 4–7 which, in addition, receive somatosensory and auditory inputs.

The visual and somatosensory projections are topographical representations of their primary receptor surfaces giving maps of visual space and body surface in the superior colliculus (Gordon, 1973, 1975; Siminoff, Schwassman & Kruger, 1966; Feldon, Feldon & Kruger, 1970; Cynader & Berman, 1972; Dräger & Hubel, 1975*a*, *b*, 1976; Stein, Magalhães-Castro & Kruger, 1976; Stein & Dixon, 1979; Tiao & Blakemore, 1976; Chalupa & Rhoades, 1977; Finlay, Schneps, Wilson & Schneider, 1978). A simple projection from the primary auditory receptor surface results, however, in a tonotopic representation, not one of auditory space. A map of auditory space has, nevertheless, been demonstrated in the mesencephalicus lateralis pars dorsalis (Knudsen & Konishi, 1978*a*) and the optic tectum (Knudsen, 1982) of the barn owl, which are the homologues of the mammalian inferior and superior colliculi respectively. Recent attempts to demonstrate directly such a map in the cat inferior colliculus (Aitkin, Semple, Calford, Phillips & Pettigrew, 1982), auditory cortex (Middlebrooks & Pettigrew, 1980*a*, *b*, 1981) or superior colliculus (Wise, Irvine, Pettigrew & Calford, 1982) have not met with success. There have, however, been indications that a rather general topographic representation of auditory space is found in the superior colliculus of several mammals. Wickelgren (1971), Gordon (1973) and Updyke (1974) have shown that the medial borders of the receptive fields of visual and auditory cells (either bimodal or closely situated) coincide, thus implying that an auditory space map is present. More often investigators have simply noted registration of the receptive fields of auditory and visual cells from the same position within this nucleus.

In the present study, we have investigated the distribution and response properties of auditory neurones in the superior colliculus of the guinea-pig. In particular, we aimed to determine whether these cells respond optimally to sounds coming from a specific spatial location and, if so, whether they are organized according to their receptive field locations so as to form a map of auditory space. In addition we wanted to know how well the auditory receptive fields correspond to those of visual neurones recorded from the same part of the superior colliculus.

## METHODS

### *Anaesthesia and surgical preparation*

Pigmented guinea-pigs weighing between 200 and 450 g were anaesthetized using a neuroleptic technique (Evans, 1979; Evans & Harrison, 1980). The tracheae were cannulated and rectal temperature was maintained at 37 °C with a thermostatically controlled heating blanket.

Following a mid-line incision, a flap of skin between the ears, the temporalis muscle on each side and the periosteum were removed to expose an area of skull extending from the coronal suture to the lambdoidal suture. A craniotomy was performed over the cortex overlying the superior colliculus extending from 4–11 mm posterior to the coronal suture and 5 mm laterally from the mid line. The animals were then mounted on a minimal head-holder which consisted of a metal bar with a flattened annular end which was screwed to the skull. The head-holder annulus surrounded the craniotomy and when sealed to the skull with dental cement provided a chamber 1–2 mm deep which, after dura removal, was filled with 2% agar to minimize brain pulsations. The pinnae were repositioned by sutures and the head-holder was adjusted so that the animals' heads assumed a normal position. The animals were then transferred to a small table at the centre of an anechoic chamber.

*Recording and analysis*

Glass-coated tungsten micro-electrodes were advanced into the superior colliculus using a remote hydraulically driven microdrive. The potentials were conventionally amplified, bandpass filtered from 500 to 5000 Hz, displayed on an oscilloscope and discriminated. The number of spikes in response to thirty-two stimulus presentations was summed using an electronic counter in a time window starting 10 ms after the stimulus onset. The duration of this counting window was varied for individual neurones as indicated in the text.

To enable histological verification of the recording site electrolytic lesions were produced by passing a tip negative current of 10 $\mu$A for 20 s through the recording electrode.

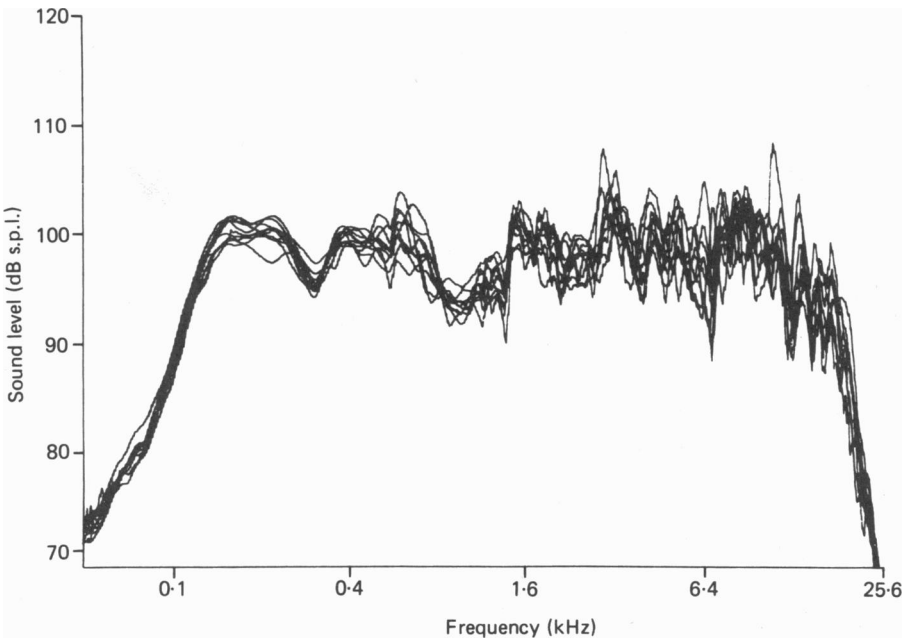


Fig. 1. Frequency *versus* sound pressure (in decibels s.p.l.) at the maximum output level for each of the eleven loudspeakers measured at the position of the centre of the animal's interaural plane with all equipment *in situ*.

*Histology*

On completion of each experiment the recording electrode was inserted into the brain in a position anterior to the superior colliculus, cut off and left *in situ* to ensure sectioning in the plane of the electrode penetrations which, because of the minimal head-holder, was somewhat variable. The brain was removed and placed in 10 % formal saline for a minimum of 3 days before being transferred to 20 % sucrose prior to embedding in egg albumin and sectioning at 50 $\mu$m on a freezing microtome. The sections were then stained with Cresyl Fast Violet. A few brains were fixed with Bouin fluid to allow the use of a fibre stain (Marsland, Glees & Erikson, 1954) for easier identification of the layers of the superior colliculus. The electrode tracks were reconstructed from the lesions and microdrive depth readings to allow identification of the recording sites.

*Stimulus generation and calibration*

(*a*) *Auditory stimuli*. Sound stimuli consisted of either tones of 100 ms duration with 5 ms rise/fall or 100 ms bursts of white noise. Continuous sine waves from an oscillator or white noise were separately gated using four quadrant multipliers, attenuated, mixed and amplified. The amplified output could be switched to any of eleven loudspeakers positioned at 22·5° intervals in a circular frame (1·1 m radius to the front of the cones) which surrounded the central table in the anechoic

chamber (Sound Attenuators Ltd. internal dimensions to tips of cones 2·6 × 3·1 × 1·9 m). The speakers were RS twin-cone units (diameter 0·165 m) in cabinets 0·305 × 0·203 × 0·130 m. Damping material was placed over the front of the cabinets except for the cone area to minimize echoes. The frequency responses of the units were measured, using a Bruel and Kjaer 12·7 mm condenser microphone and 2610 amplifier, at 20 cm in front of each speaker and also at the position of the centre of the animals' interaural plane with all equipment, including the microdrive and blanket, in position. The sound levels near the speakers showed less variability than those at the interaural plane, indicating that the equipment produced some distortion of the sound field. The frequency responses at the interaural plane are shown in Fig. 1. Although the sound level varies with frequency (±8 dB from 100–20000 Hz), more important for the present data is the variability between the eleven units at any frequency – this is generally about ±3 dB. The loudspeaker response determined the band width and level of the noise signal. The mean maximum r.m.s. sound pressure of the noise signal from the speakers was 83 dB s.p.l. (sound pressure level) (S.D. 1·58 dB) measured at the position of the centre of the guinea-pig's interaural plane.

Four animals were used to form an estimate of the effect of head shadow, pinna, concha, and meatus on the sound pressure at the tympanic membrane. These animals were anaesthetized, mounted in the head-holder and a 1 mm probe tube microphone (Bruel and Kjaer 4134) was positioned, from behind, close to the tympanic membrane via a small slit in the posterior wall of the external auditory meatus. The sound pressure was measured at nine frequencies in octave steps from 100–25600 Hz. The same microphone was then used to measure the sound pressure at the position of the centre of the interaural plane with the animals removed. Differences between these two measurements were taken as indications of the effects of head shadow and meatus, thus eliminating the need to take into account the frequency response of the probe microphone assembly.

A specially constructed microprocessor controller was used to plot frequency/intensity response areas in detail. This unit controlled the oscillator frequency to produce a sequence of sixty-four 100 ms tone bursts equally spaced on a logarithmic scale. At each frequency the number of discharges evoked by a single presentation was counted and plotted as a histogram on an X–Y recorder. On completion of each set of sixty-four bursts the stimulus intensity was increased by 5 dB and the sequence repeated. Eight intensity steps were used to investigate the response area over 40 dB (see Fig. 4 for an example).

(*b*) *Visual stimuli.* During experiments conducted in the anechoic chamber, the centre of the receptive fields (r.f.s) of visually responsive cells in the superficial layers of the superior colliculus was determined using a flashing light which produced a vigorous discharge with a latency of 50–60 ms. The light was moved by hand until the centre of the r.f. was found.

Under anaesthesia the eye of the guinea-pig is not normally positioned, but is rotated forwards and downwards. Any assessment of r.f. position must take this into account since the tectal visual representation is retinotopic. We found that retinal landmarks such as the optic disc are not sufficiently prominent even in unanaesthetized guinea-pigs to be usable. This appears to be peculiar to guinea-pigs (no difficulty was found with other rodents) and in our opinion was not due to cloudiness of the cornea. We therefore determined the optic axis using the Purkinje–Sanson series of images by aligning the multiple reflexions of an ophthalmoscope and back reflecting the beam onto the wall of the chamber. This procedure was performed after the r.f. determination in every electrode penetration.

We used four conscious hand-held guinea-pigs to estimate the normal eye position in our experimental reference frame. The normal position of the guinea-pig eye from such determinations was 17·7° elevation (S.D. 3·9°), 73° azimuth (S.D. 7·7°); 0° elevation is level with the animal's interaural plane and 0° azimuth is directly in front of the animal. As a comparison the eye position in eighteen determinations from four anaesthetized guinea-pigs was −3·9° (S.D. 5·4°) elevation, 62·6° (S.D. 7·9°) azimuth. Thus (although admittedly a limited sample) the eye of an anaesthetized guinea-pig is tilted forward by an average of 10·4° and downwards by 21·6°. Because of the eye position the visual r.f. data obtained in the auditory experiments were of limited use for addressing the question of the registration of visual and auditory maps. We obtained a more controlled and detailed map of the visual projection in four animals. Using the same anaesthetic, without paralysis, the contralateral eyelid was removed, and the eye centred to a subjectively normal position by attaching sutures to the conjunctiva. This procedure was adequate to prevent significant eye movements (repeated determinations of the optic axis were consistent and receptive-field positions were reproducible). The pupil was dilated with atropine and the eye kept moist during the

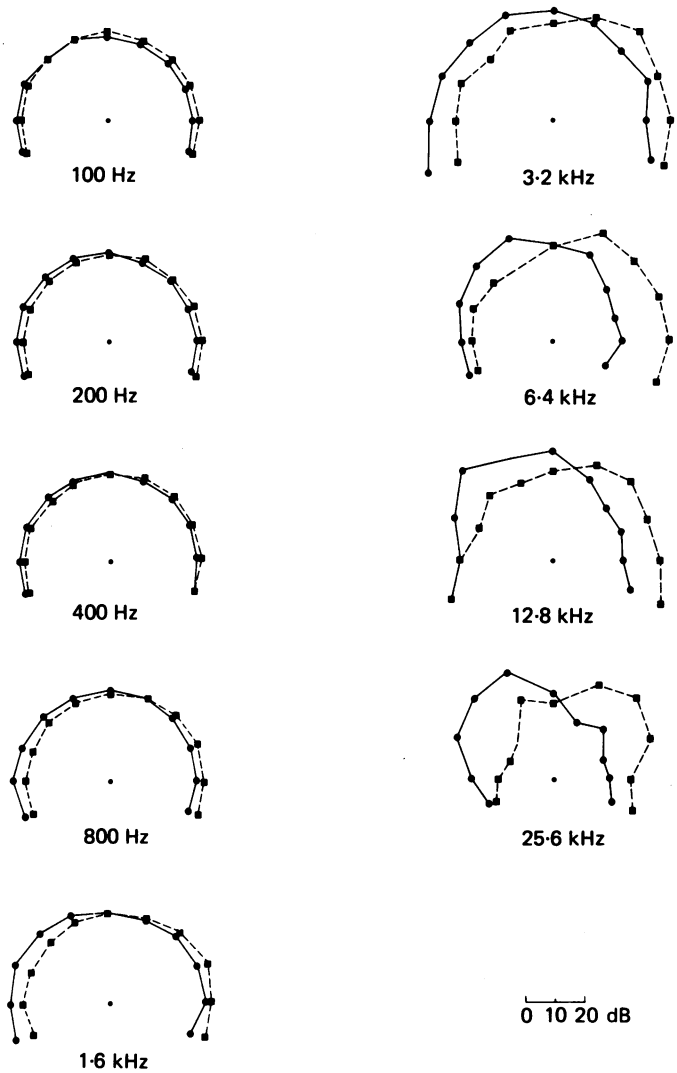


Fig. 2. Polar diagrams with sound pressure at the tympanic membrane relative to the sound pressure at the position of the centre of the animal's interaural plane plotted on the radial axis for tonal stimuli delivered from each of the eleven loudspeakers. The sound pressures at the right tympanic membrane are indicated by the filled squares and dashed lines and those at the left by filled circles and continuous lines. Mean of four animals.

experiment with mineral oil. The ipsilateral eyelids were sutured together to ensure that the stimulation was entirely contralateral. The visual map was then determined using an Aimark perimeter centred on the optic axis.

Each superior colliculus was explored with electrode penetrations at 300 $\mu$m intervals in the rostro-caudal direction and in 500 $\mu$m steps medio-laterally. We measured the centre of the receptive fields of multi- or single unit activity in the superficial layers using a 2·8° white spot and checked each with a similar sized hand-held black spot. A complete study required about ninety penetrations per animal. We adjusted the stereotaxic co-ordinates to fit a standard dorsal view of the superior colliculus using histological reconstructions and electrolytic lesions.

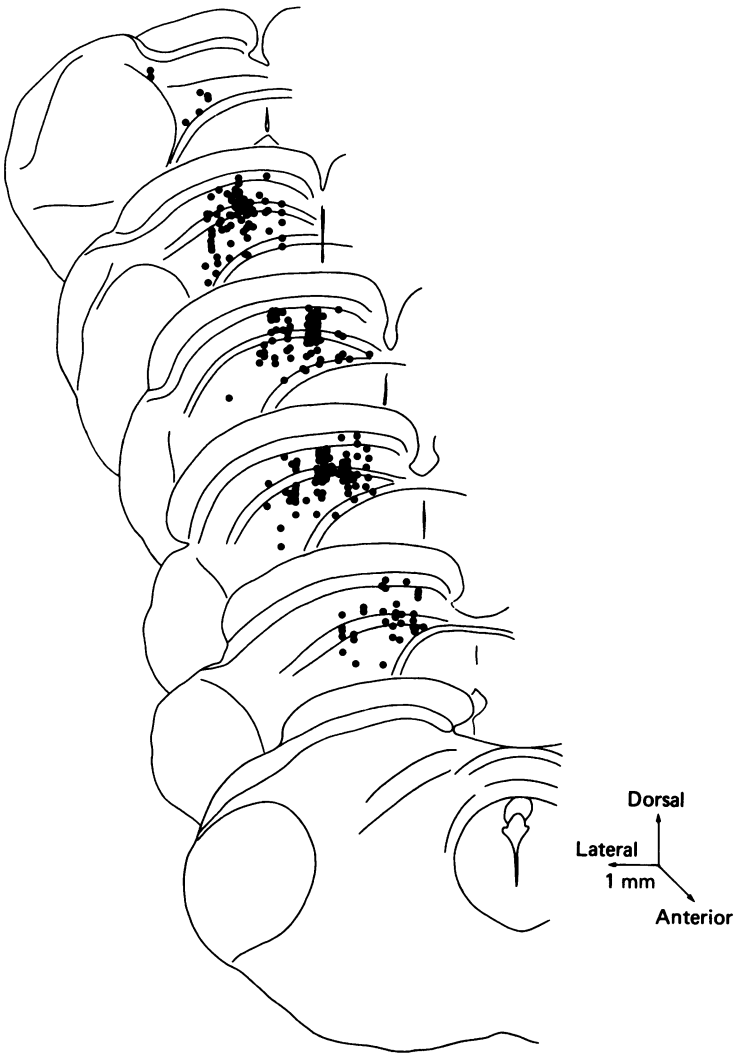


Fig. 3. Camera lucida drawings of serial transverse sections through the superior colliculus at 0·5 mm intervals with the laminae indicated and showing the position of all cells which responded to auditory stimulation and whose position was histologically verified. In transposing the data onto a single set of sections allowances were made for shrinkage, differences in the plane of the electrode and variations between animals.

## RESULTS

### *Pinna, concha and head shadow effects*

Owing to the shadowing effect of the head and reflexions within the pinna and concha, the sound pressure reaching the tympanic membrane depends upon the direction from which the sound originates. Even without further neural processing therefore, these physical effects will produce a monaural bias toward the ipsilateral side for high frequencies. Fig. 2 illustrates the relative sound pressure produced at

the tympanic membrane by free-field tonal stimuli (see Methods for details) with the animals facing the centre of the array of speakers. These effects were progressively more profound as the frequency was increased. At 100 Hz the eardrum sound pressure due to ipsilateral sounds exceeded the mid-line position by less than 0·5 dB and that due to contralateral sound was lower by the same amount. The deviations amounted to no more than $\pm 2$ dB up to 800 Hz. Above this frequency the effects began to be more pronounced, reaching $\pm 10$ dB or more at the highest frequency.

*Laminar distribution of auditory neurones in the superior colliculus*

We have adopted the terminology used by Kanaseki & Sprague (1974) in the cat and by Sidman, Angevine & Pierce (1971) in the mouse to describe the seven laminae in the superior colliculus.

Plate 1 shows a photomicrograph of a transverse section through the guinea-pig superior colliculus containing two electrolytic lesions, each at the site of auditory neurones. The diagrammatic section on the right hand side of the plate illustrates the position of the seven layers.

Fig. 3 shows camera lucida drawings of transverse sections through the guinea-pig superior colliculus at 0·5 mm intervals, onto which we have plotted the position of neurones responding to auditory stimulation. We have recorded from auditory neurones located throughout the deep layers. Layer 3 has usually been considered to be an entirely visual area but, as shown in Fig. 3, several auditory neurones have been found here. Since we have not investigated somatosensory cells at all we do not have any direct evidence to suggest a clustering of the different modalities in a single track as suggested by Dräger & Hubel (1975*b*). There were, however, indications that driving of the background activity was not continuous during a penetration but occurred most strongly at depths separated by insensitive regions. These silent regions may have represented areas of sensitivity to other modalities or passage of the electrode through fibre layers.

*Response properties of superior colliculus auditory neurones*

We have recorded from 317 cells which responded to auditory stimuli and which were located in superior colliculus. Of these 282 cells were held long enough for analysis of their response properties. Superior colliculus auditory neurones almost invariably responded to the onset of the noise or tone burst and the most common response consisted only of one or a few spikes. We have occasionally encountered more sustained responses occurring over a period of tens or hundreds of milliseconds and also neurones responding to both the onset and offset of the auditory stimulus. The latency from the arrival of the sound at the ear to the first neural spike was quite short, ranging from 7–27 ms (cf. the values of 10–20 ms from the cat superior colliculus obtained by Wise & Irvine, 1981).

The minimum threshold to the noise stimulus depended on the direction of the sound source (see later for details). For stimulation with the most effective speaker, the noise thresholds ranged from 13–28 dB s.p.l. (r.m.s. noise level re 20 $\mu$Pa). The detailed response areas were plotted for forty-five neurones. Fig. 4 shows one example response area with a characteristic frequency of 17·5 kHz at 10 dB s.p.l. (other examples may be found in Fig. 6). At threshold sound levels the neurone in Fig. 4

responded only to frequencies at or near 17·5 kHz whilst at higher stimulus levels it responded to a wide range of frequencies forming a roughly triangular shaped response area. Although we have found simple tuning curves such as this, as common, even in our limited sample, were complex tuning curves with several frequency peaks or even broad response areas covering many octaves. These complex response areas are unlikely to be due to the variation in output of the speakers which all have fairly

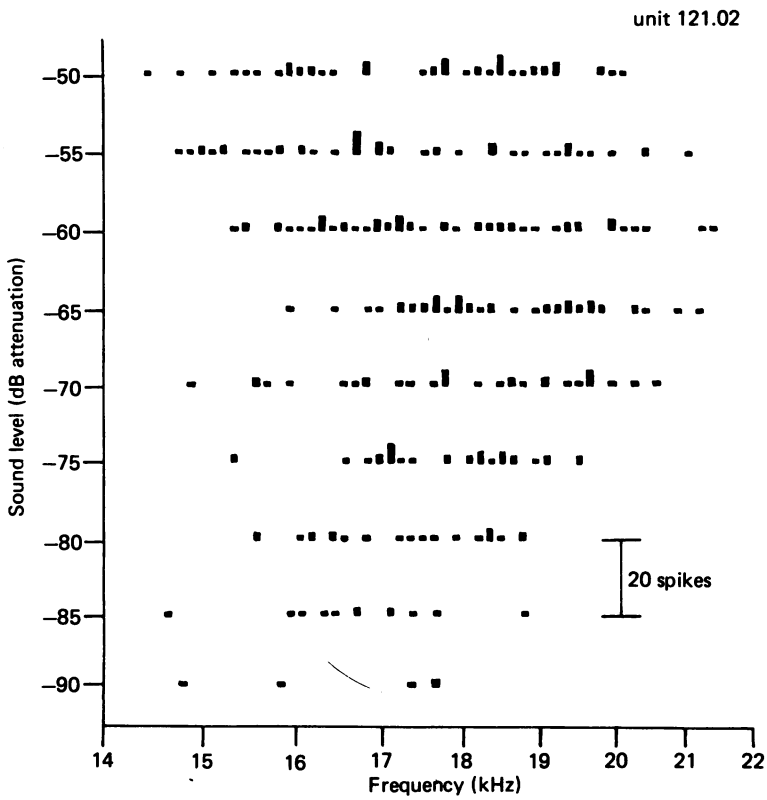


Fig. 4. Frequency response area of a single cell in the superior colliculus. Each bar represents the number of spikes in response to a single presentation of a 100 ms tone burst of the appropriate frequency and intensity.

flat frequency responses (see Fig. 1). The majority of cells had thresholds to tones of 10–50 dB s.p.l. It was often difficult to assign a single characteristic frequency, however, where this was possible, the values ranged from 1·4 to 25 kHz. No attempt was made in the present study to investigate tonotopicity in this nucleus.

It is noticeable in Fig. 4 that even the strongest responses were only of a few spikes and were quite unreliable. We have found that superior colliculus auditory neurones habituate with short interstimulus intervals (of up to 600 ms). Extending the interstimulus interval increased the reliability, reaching an optimum response at an interval of 1·5–2·5 s, but further extension beyond this interval did not produce secure firing to every stimulus. The spike rates in the later polar diagrams therefore are frequently an indication of discharge probability (often 50 % or less), rather than

discharge rate *per se*. Increasing the noise stimulus intensity usually increased the number of spikes and the response reliability, but non-monotonicity was also frequently observed with fewer spikes elicited by higher than by lower intensity stimuli (examples are shown in Fig. 5).

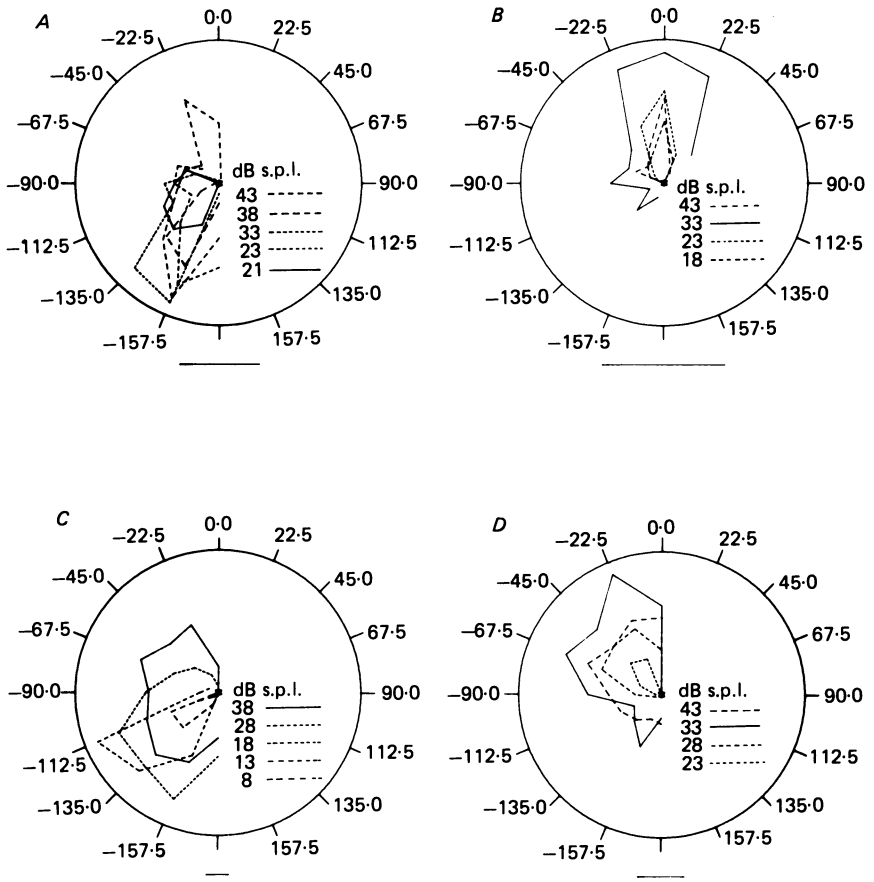


Fig. 5. Responses of four superior colliculus auditory cells to a 100 ms burst of white noise as a function of the horizontal location of a sound source and its level. Each value plotted on the radial axis is the mean number of spikes elicited by thirty-two stimulus repetitions. The optimum repetition intervals (see text) for these four cells were 900, 1800, 1000 and 1900 ms respectively. Only spikes occurring 10–70 ms after the stimulus onset were counted to minimize the contribution of spontaneous discharges. The bar represents 0·5 counts per presentation.

*Sensitivity of superior colliculus auditory neurones to sound location*

The data which we have obtained in this study indicate a precise topographically organized representation of auditory space in the superior colliculus. We have investigated the response of 244 neurones as a function of the location of a burst of white noise; 73 % of these responded more strongly or more reliably when a sound originated from a particular location. This was especially so for sounds close to the threshold of the neurone. A total of 134 neurones was held for long enough to

determine the effect of stimulus intensity upon this spatial tuning, revealing two very different classes of neurone. Fig. 5 illustrates two examples of neurones from different animals whose spatial tuning was relatively unchanged with increase in stimulus intensity (37 % of those analysed). In Fig. 5*A* the neurone responded to sounds from a limited spatial angle at 157·5°, almost directly behind the animal and in Fig. 5*B* at 0°, which is in front of the animal. These preferred sound locations were maintained even with stimulus levels up to 35 dB above threshold. Fig. 5*C* and *D* illustrates two

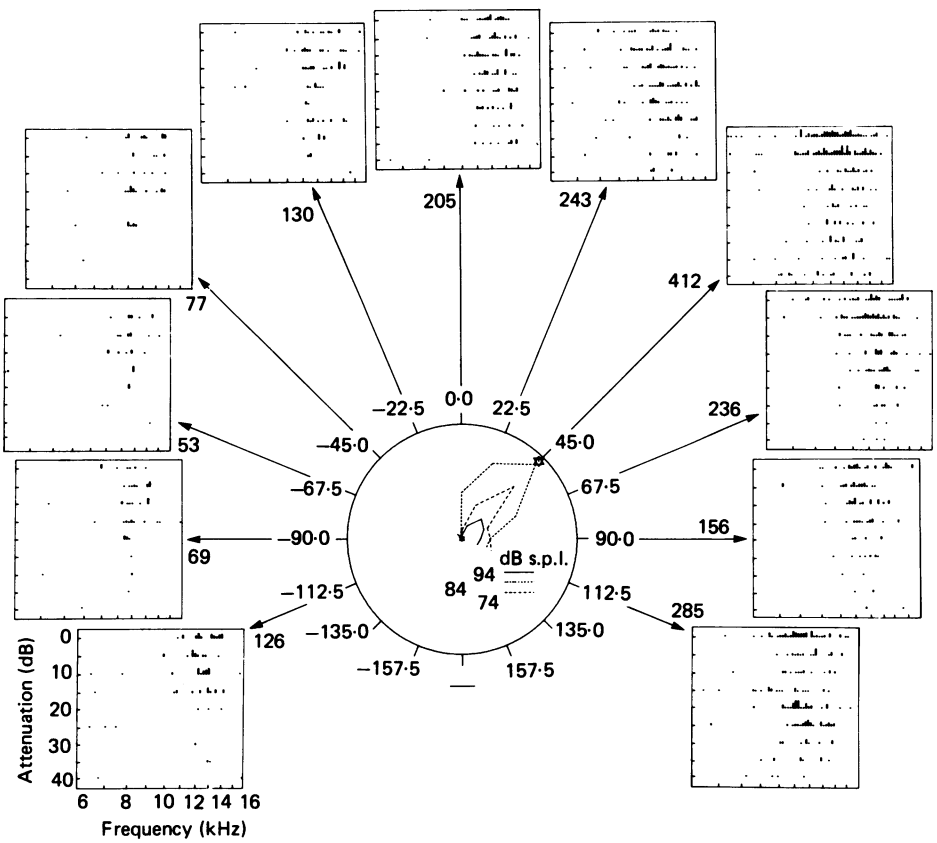


Fig. 6. Polar diagram (as Fig. 5) of a cell in the left superior colliculus showing a preference for sounds at 45° azimuth. The frequency response areas were measured from each of the eleven loudspeakers as indicated. The axis markers on the abscissa indicate 1 kHz steps from 6–16 kHz. The ordinate markers are 5 dB steps. The figures near the arrowheads indicate the total number of spikes in each of the response areas. Star shows visual r.f. position.

examples of neurones whose spatial tuning only existed for sounds within a few decibels of threshold (63 % of our sample), again with one responding to sounds coming from behind and the other from in front of the animal. For these neurones an increase in sound level of only a few decibels caused a rapid expansion of the effective stimulus locations, particularly in the caudal direction, in many cases extending over most or all of the contralateral hemifield at levels even 10 dB above threshold.

We have found intermediate response types but most fell into one or other of the two types described above. The cell in Fig. 5*A* has a two-lobed polar diagram at 43 dB s.p.l. with the major lobe behind and the smaller lobe diametrically opposite. Cells with bilobed polar diagrams were located in areas of the superior colliculus which we associated (see next section) with responses to sounds from the direction indicated by the major lobe direction.

Within a single electrode penetration, all cells showing spatially tuned responses, whether or not this tuning was tolerant of intensity changes, responded to sounds from the same location (as shown in Fig. 7). More than one auditory cell was found in sixty-five out of ninety-one penetrations.

Although noise was a more effective stimulus, the preferred sound location could also be determined using tonal stimulation. Fig. 6 illustrates a neurone for which a polar diagram to white noise was plotted together with response areas to tones from each loudspeaker. The polar diagram reveals a clear preferred sound location in the contralateral hemifield, which was unchanged as the stimulus level was increased. All of the eleven response areas indicate that the neurone responded best to frequencies at or near 12 kHz and had a fairly simple 'V' shaped response area. Even at best frequency this unit only responded sporadically, but the responses to contralateral sound sources are clearly stronger than those from ipsilateral sources. In terms of lowest threshold, most spikes for a single stimulus presentation and most frequency/intensity combinations eliciting spikes, the response to sound from 45° contralateral is strongest. This is emphasized by comparison of the total number of discharges evoked during the determination of each response area as indicated by the numbers next to the arrowheads; stimulation from 45° produced 412 spikes compared to the next strongest response of 285 spikes. We have reported (Palmer & King, 1982) that sounds in the ipsilateral field did not drive superior colliculus cells. Fig. 6 indicates that although this is certainly true for noise stimulation (see Fig. 5), tonal stimulation from ipsilateral locations will drive a neurone. Spatial tuning to tonal stimulation, although certainly demonstrable, would therefore appear to be somewhat less well defined than to noise stimulation.

We emphasize here that with speakers at set intervals we are sampling the receptive fields at discrete points. This may cause distortion of the shape and blurring of the organization if the field is narrower than 22·5° and not located at a speaker position. In addition, sampling only in the horizontal plane may cause inaccuracy in specification of position for receptive fields with centres at other elevations and may result in weaker responses than to centrally located stimuli.

*Distribution within the superior colliculus of spatially tuned auditory neurones: an auditory space map*

When sequential electrode penetrations were made in a single animal in a rostro-caudal direction, the location of sounds to which cells in each track responded most vigorously moved progressively from the anterior to the posterior part of the contralateral auditory field of the animal. Fig. 7 shows data from a single animal in which cells from six electrode penetrations were analysed. For each penetration one polar diagram at a single noise level (usually near threshold) is shown for each of nineteen auditory cells. There is a clear monotonic sequence: the most posterior

penetration yielded cells (Fig. 7*P–S*) responding to sounds at 157·5° azimuth, while the most anterior penetration only gave one cell (Fig. 7*A*) responding best to sounds directly in front of the animal. Of the data shown in Fig. 7, those in Fig. 7*A–D*, *G*, *K–S* could all be described as showing a definite single preferred sound location to which responses were strongest or most reliable. Of the remainder, Fig. 7*E*, *H*, *J* had broad fields at the sound levels we were able to use (for Fig. 7*E* and *H* the

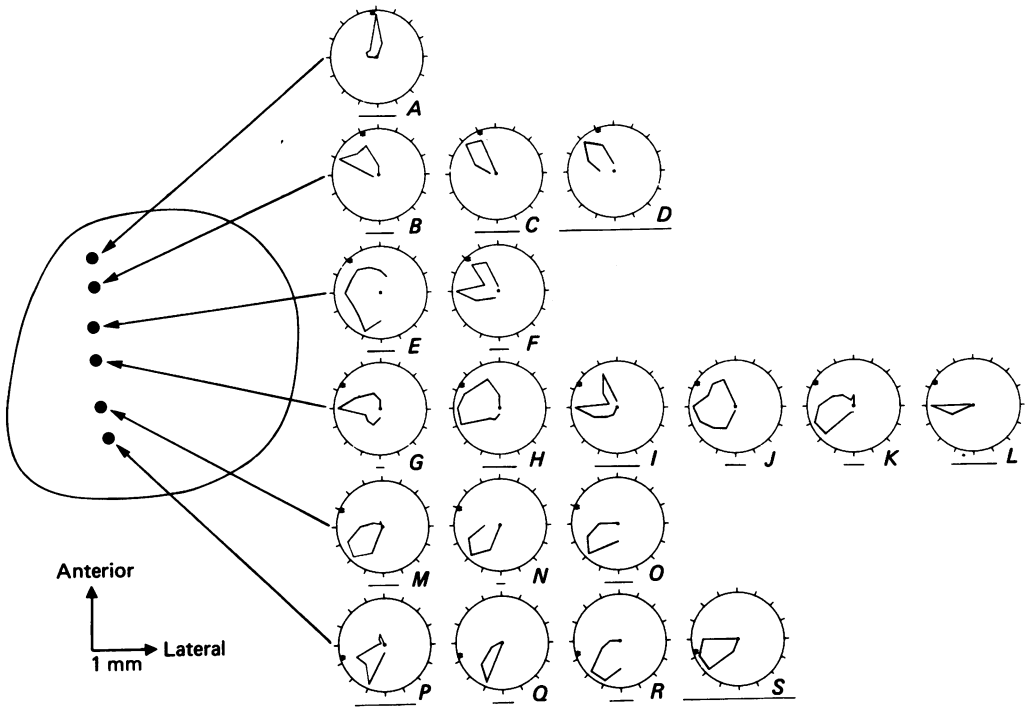


Fig. 7. Surface view of the right superior colliculus showing the location of six electrode penetrations. Polar diagrams are shown for all cells in these six penetrations for which data were obtained. Each polar diagram is for a single sound level at which the cell's response was most tuned for spatial location. This sound level was usually near threshold (see text) except for a few cells for which data at only a single high stimulus level was collected.

cells were only held for the sound level shown), and Fig. 7*F* and *I* had two well-defined lobes. The two lobes of the cell in Fig. 7*F* straddled the direction predicted from the otherwise monotonic sequence of tuned cells. The larger lobe in Fig. 7*I* points in the same direction as the tuned single lobed cells in the same track. The yield in these experiments has been generally low and extensive data such as those in Fig. 7 were not obtained from the majority of animals. The same topographical organization can be observed, however, in pooled data as indicated in Fig. 8. Fig. 8*A* shows the location of 142 spatially tuned cells with the different symbols indicating the preferred sound direction. Obviously such pooling introduces unavoidable inaccuracy which, to some extent, obscures the monotonicity shown in Fig. 7. Nevertheless, Fig. 8*A* still demonstrates a topographically ordered map of auditory space in the guinea-pig superior colliculus. The auditory projection does not, however, extend over the whole

of the tectum. The open square symbols in Fig. 8*A* indicate seventeen electrode penetrations through the anterior superior colliculus which, although giving visual responses in the superficial layers and definitely passing through the deeper layers, did not yield auditory responsive cells. Fig. 8*B* is an identical surface view of the superior colliculus on which the locations of only those cells whose spatial tuning did not broaden with intensity (Fig. 5*A*, *B*) are shown. This subset of cells are clearly organized in the same topographical sequence.

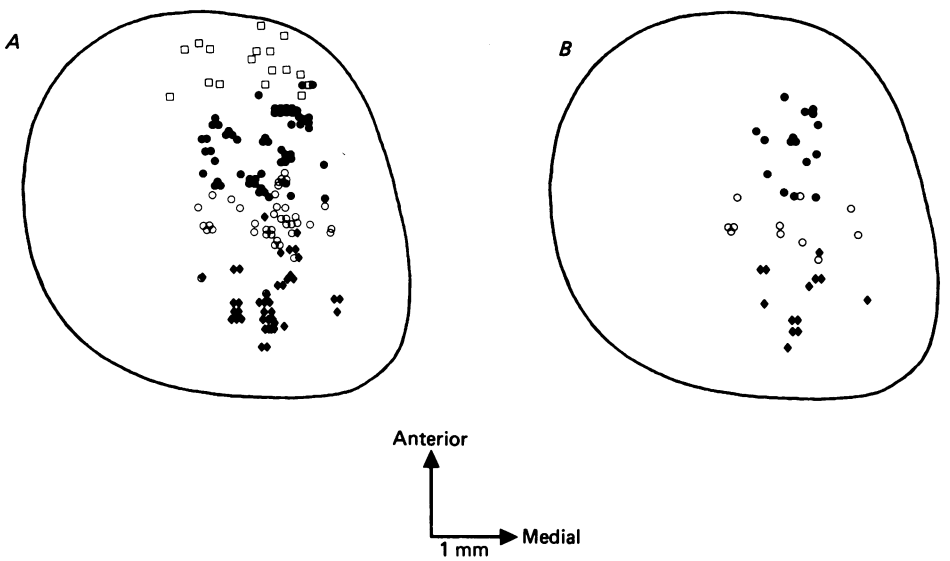


Fig. 8. Two identical surface views of the left superior colliculus. The open squares in Fig. 8*A* indicate the position of electrode penetrations in which visual responses in the superficial layers were observed, but no auditory responses could be detected in the deeper layers. Filled circles, open circles and filled diamonds indicate respectively the positions of cells which showed a preferrence for sounds located at 0–45°, 67·5–90° and 112·5–157·5° azimuth. Fig. 8*B* shows a similar plot only for those cells whose spatial tuning did not broaden rapidly with stimulus intensity (as in Fig. 5*A*, *B*); symbols as in Fig. 8*A*. In both Fig. 8*A* and *B* we have combined data obtained from cells in the left and right colliculi; all responses were almost entirely contralateral with the spatial fields in the two colliculi showing mirror-image symmetry about the mid line.

*Retinotopic representation in the superficial layers of the superior colliculus*

We have determined the retinotopic organization of the guinea-pig superior colliculus because no data for this species has previously been available. We stress, however, that the data presented here are not definitive, since, whilst we were able to centre the Aimark perimeter on the optic axis, the lack of definable retinal landmarks did not allow adjustment of the map for eye rotation.

All four animals gave very similar maps with slight differences due perhaps to eye alignment or rotation errors. The data from a single animal are shown in Fig. 9. Fig. 9*A* shows a perimeter card with the receptive field positions measured for each of the electrode penetrations which are indicated by the dots on the dorsal view of the superior colliculus in Fig. 9*B*; the open circles indicate absence of visual activity. From the data of Fig. 9*A* we have constructed 10° iso-contour lines in the visual field

relative to the optic axis (thin lines) and the vertical and horizontal meridians (thick lines).

The retinotopic projection to the guinea-pig superior colliculus is very similar to that of most other vertebrates (Sprague *et al.* 1973; Kruger, 1970). The superior visual field is represented in medial parts of the superior colliculus and as the electrode was moved more laterally the position of the receptive fields represented moved more inferior. Temporal visual field is represented in the caudal regions and nasal visual field in the rostral regions.

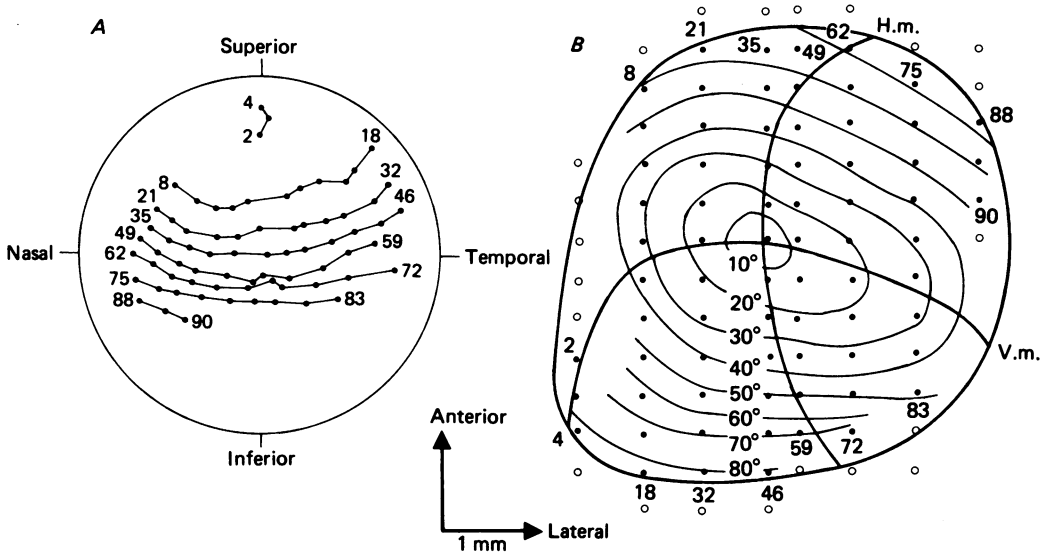


Fig. 9. *A* shows a visual perimeter card on which the positions of visual receptive fields from seventy-two electrode penetrations have been marked for the left eye with the perimeter centred on its optic axis. Successive penetrations in the rostro-caudal direction have been connected. *B* shows a dorsal surface view of the right superior colliculus showing the positions of the electrode penetrations. The filled circles are the positions at which visual responses were found and the unfilled circles those in which no visual responses were observed. Penetrations in *A* and *B* are identified by numbers at the front and back of each series. The visual space contour lines (thin lines) and the vertical and horizontal meridia (V.m. and H.m. respectively; thick lines) have been constructed from the perimeter card.

## DISCUSSION

The present study using free-field acoustic stimuli under anechoic conditions has demonstrated that cells in the guinea-pig superior colliculus are able to signal the location of a sound source in the horizontal plane. The distribution of these location sensitive cells within the superior colliculus is such as to produce a topographic representation of this dimension of auditory space.

### *Response properties and preferred sound locations*

In many important respects the data presented in this paper are consistent with earlier reports but differ from some more recent attempts to demonstrate an auditory space map. The latencies which we have found (to the first spike), the temporal

response patterns and the propensity for cells to habituate rapidly are all consistent with other studies (Allon & Wollberg, 1978; Wise & Irvine, 1981; Horn & Hill, 1966). In cells showing erratic firing, doubling or trebling the inter-stimulus interval did not produce secure firing to every stimulus. This finding is at first sight quite surprising. We did not, however, use inter-stimulus intervals exceeding 2–3 s since to do so would have increased analysis times unacceptably. Thus it seems possible that secure firing to every stimulus might have been achieved with even less frequent stimulation. In general, the responses which we have found were not as strong as those shown by Gordon (1973, Figs. 16 and 17) in cat superior colliculus. These relatively vigorous responses were obtained using a noise source moving in the receptive field. One might speculate, therefore, that at least part of the reason for the weak sporadic nature of some of the responses might have been inappropriate use of stationary stimuli in a nucleus which seems to be most sensitive to moving stimuli of other modalities (e.g. Stein & Gordon, 1981; Clemo & Stein, 1982). There have been several good indications of a topographical representation of auditory space in the superior colliculus (Wickelgren, 1971; Gordon, 1973; Updyke, 1974; Dräger & Hubel, 1975*a*, *b*; Harris, Blakemore & Donaghy, 1980; Chalupa & Rhoades, 1977; Tiao & Blakemore, 1976), although these have been mainly based on limited samples of auditory responsive neurones. The general conclusion of these studies was that the auditory fields were rather broad and ill-defined and topographical organization was only suggested by either co-incidence of visual and auditory fields or by plotting the co-variation of the medial borders of the visual and auditory fields. In both cases the topographical arrangement was inferred from a knowledge of the well organized visual projection. Our data reveal well-defined auditory fields (in many cases) and demonstrate their topographical arrangement directly rather than by inference. There are at least three probable sources of the differences in sharpness of spatial tuning between our data and those of some earlier studies: (1) The use in many of the previous studies of uncontrolled auditory stimulation (e.g. noise generated by blowing air through a tube). (2) The selection of bimodal cells to enable inference from the visual response – it is possible that bimodal cells may represent a sub-population not as well tuned as unimodal cells. This seems somewhat unlikely, however, in the light of the recent finding (Knudsen, 1982) that 90 % of the cells forming a precise auditory space map in the barn owl optic tectum are bimodal. We did not test auditory neurones for responsiveness to other modalities but multimodal cells must certainly be included in our sample. (3) The smaller samples may not have included cells well tuned at the sound levels used (cells maintaining tuning at high intensities were only 37 % of our sample).

The frequent finding of a second oppositely directed lobe in the polar diagrams of cells responding to sounds in front of or behind the animal (Fig. 5*A*) deserves further comment. In psychophysical studies of sound localization, subjects often identify the location of a sound from directly in front as coming from behind and vice versa, particularly if the sounds have low frequency content (Stevens & Newman, 1936). This front/back ambiguity is caused by the lack of differences in the signals reaching the two ears. The bilobed cells often responded almost equally to sounds from in front and behind the animal and could conceivably represent a physiological homologue of the psychophysically observed front/back reversal phenomenon.

Although there have been numerous investigations of the coding of binaural cues for localization (see Erulkar, 1972 for references), the use of free-field stimulation to directly investigate localization has been limited. Despite the elegant demonstration of very precise auditory space maps in the auditory mid-brain and optic tectum of the barn owl (Knudsen & Konishi, 1978*a*, *b*; Knudsen, 1982), attempts to demonstrate directly similar organization in the mammal have not so far met with success. Several groups using the cat have described consistent responses to free-field stimulation in inferior colliculus (Aitkin *et al.* 1982), auditory cortex (Middlebrooks & Pettigrew, 1980*a*, *b*, 1981) and indeed in superior colliculus (Wise *et al.* 1982). At these three sites the cells were initially grouped into those responding equally to sounds from all directions, those responding to sounds anywhere in the contralateral hemi-field and those with small spatial receptive fields. The fields of this latter group of cells were all located along the acoustic axis of the contralateral pinna; movement of the pinna caused movement of the field position (Middlebrooks & Pettigrew, 1981). It was therefore concluded that whilst circumscribed auditory fields existed, they reflected the pinna effect and were not therefore an adequate basis for a neural space map *per se*. More recently, it has been demonstrated that the three response types represent a continuum of pinna effects at different frequencies and the initial classification represented the response of cells differing in their frequency sensitivities (Semple, Aitkin, Calford, Pettigrew & Phillips, 1983; Addison, Aitkin, Moore & Semple, 1983).

Given the internal consistency of these free-field studies and the differences in their conclusions from those of the present study, it is essential to demonstrate that our findings do not represent responses to spurious cues from the multiple transducers or from a combination of multiple speakers, pinna effects and tonotopicity. Examination of Fig. 1 demonstrates that whilst the loudspeakers were reasonably well matched, there were differences in the exact frequencies of the individual peaks. For these transducer differences to be responsible for the monotonic rostro-caudal change in preferred sound location, the differences would also have to change progressively and no such trends were evident in the individual calibration curves. Further arguments against spurious cues from the sound system are that the progression in preferred location was resistant to changes in the order of the loudspeakers and that a mirror image progression was found in the opposite colliculus. Even given a rather small difference in transducer output which changed monotonically it would require a strict tonotopic organization for these to be translated into a spatial sequence of sound positions. Our frequency–response area data, although not specifically addressing this question, suggest that tonotopicity in the superior colliculus, if present, must be rather ill-defined due to the presence of cells with broad and multi-peaked response areas.

The pinna of the cat is a highly convoluted mobile appendage. Its mobility is readily demonstrated by the large movement toward a sound which constitutes the cat's Preyer reflex. The guinea-pig pinna is less convoluted (more like the human) and is virtually immobile; the Preyer reflex is a mere twitch. In our experiments the limited mobility was further restricted by anaesthesia and removal of much of the responsible musculature. We can therefore be certain that movements of the pinna did not cause the shift in preferred sound location. The guinea-pig pinna produces frequency-dependent enhancement and attenuation in the sound pressure at the

tympanic membrane (see Fig. 2), which result in an acoustic axis like that which has been described in detail for the cat (Phillips, Calford, Pettigrew, Aitkin & Semple, 1982). From Fig. 2 it appears, however, that the acoustic axis only becomes significant for sounds in excess of 3·2 kHz and is only pronounced for high frequency sounds. The direction of the greatest enhancement of the sound pressure at the ipsilateral tympanic membrane is centred at 45° azimuth and is quite broad even for high frequencies. Whilst we cannot guarantee that the acoustic axis was consistently positioned across animals, within the single animal shown in Fig. 7 the axis would have been constant. Differences in the acoustic axis (if affecting the responses at all) and differences in transducers may well have contributed to the variability shown in the pooled data.

Our horizontal array of speakers probably does not encompass the vertical centre of the acoustic axis (if positioned in guinea-pig as in cat) and in view of this the broadness of the pinna effect shown in Fig. 2 is somewhat surprising if we are merely cutting across the lower edge of the axis. Nevertheless, many of our responses (at least near threshold) are much more sharply tuned than the polar diagrams in Fig. 2. This and the presence of fields far anterior and posterior to the acoustic axis (Fig. 7) again suggest that the pinna does not constitute a major determinant of the responses we have observed.

Finally, the superior colliculus has been suggested as a centre for initiating head, neck and pinna movements in response to novel stimuli. To accomplish such a function the source of a sound needs to be located independently of the pinna movement in order to provide the basis for the secondary movement of the pinna to 'home' in on the sound source.

*Visual and auditory maps*

It is apparent from Figs. 7, 8 and 9 that the visual and auditory projections are broadly similar in their arrangement with fields in front of the animal located in rostral colliculus and fields in the posterior hemifield located caudally. Consideration of the exact details of registration are, however, quite problematic. We previously suggested (Palmer & King, 1982) that occasional severe discrepancies of up to 60° between visual and auditory fields were due to the abnormal eye position under anaesthesia, the absence of auditory responses in the rostral pole of the superior colliculus and sampling errors due to the curvature of the collicular surface.

The determination of the visual map in detail should provide a much better basis for consideration of the registration of the auditory and visual projections. However, whilst some comparisons can be drawn, perusal of the visual maps reveals that our conclusions in regard to registration can at best only be tentative due to the severe limitation imposed by the one dimensional array of loudspeakers.

To make a comparison of the two maps the visual contours of Fig. 9*B* have been transformed mathematically from the eye-centred co-ordinates to the same head-centred co-ordinates as the auditory data and also plotted as the mirror image onto the left colliculus as shown in Fig. 10. The contours in Fig. 10 indicate the position of the visual fields with respect to the animal's head and therefore extend from 0° (in front of the animal) to over 130° (well into the posterior of the visual field). Also shown in this Figure is the rostro-caudal extent over which our pooled samples of

auditory neurones with different preferred locations were found. Taken at face value, these data would appear to allow the following conclusions: (1) Neurones responding best to sounds in the central part of the contralateral hemifield were found in rostro-caudal superior colliculus positions corresponding to those of visually responsive cells with receptive fields in the same spatial location. (2) Neurones with auditory fields at extreme rostral or caudal positions appeared to be found in regions of superior colliculus more central than their visual counterparts, thus producing a gap in the

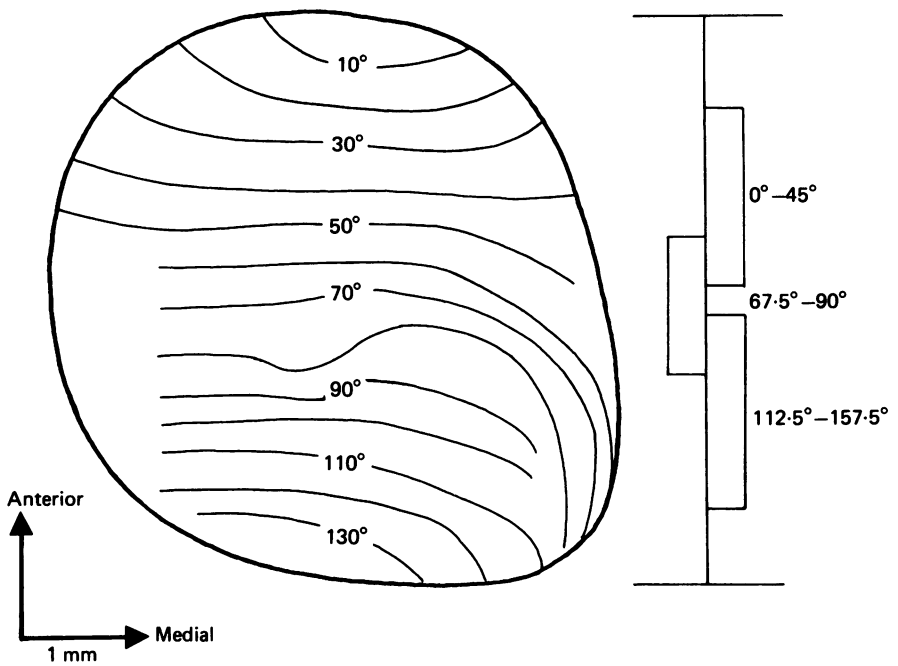


Fig. 10. Dorsal surface view of the superior colliculus showing visual contour lines with respect to head-centred co-ordinates obtained by transformation of the data from Fig. 9. Also shown is the rostro-caudal extent over which cells with the various preferred sound locations were found in our pooled data.

auditory field representation at the front of the colliculus and a lack of registration at the back. The gaps in the auditory representation may result from inappropriate positioning of the auditory stimulus for cells in those regions of the superior colliculus. This suggestion is weakened by two observations: (1) as shown in Fig. 8*A* we found no auditory activity in electrode penetrations which extended to quite lateral regions of the rostral colliculus and (2) we have found cells with auditory fields in extreme regions of the auditory hemifield even in our medial colliculus penetrations (Figs. 5, 7). A further corollary of these observations might well be an indication that the auditory fields may not be as well circumscribed in the vertical dimension as in the horizontal.

Although the auditory and visual space maps in the superior colliculus are similar, there are indications that the two maps are not co-extensive and may not be in register for extreme receptive field positions. Absence of auditory responses in rostral

superior colliculus where frontal visual space is represented has been demonstrated by other authors (Chalupa & Rhoades, 1977; Dräger & Hubel, 1975*b*). In contrast, auditory responses are found throughout the optic tectum of the barn owl (Knudsen, 1982), but even in this structure, whilst the maps are in good register, there are discrepancies in the areas of visual and auditory space represented at posterior and ventral positions.

We do not as yet know what auditory cues are responsible for this sensitivity to sound location. Nevertheless, the very presence of an auditory space map testifies to complex developmental strategies which must have been employed to organize the neural connexions. The reorganization of the auditory projection into a space map, rather than one based on a topographic representation of the receptor surface, may be essential for the function of the superior colliculus in producing motor responses appropriate to the sensory input.

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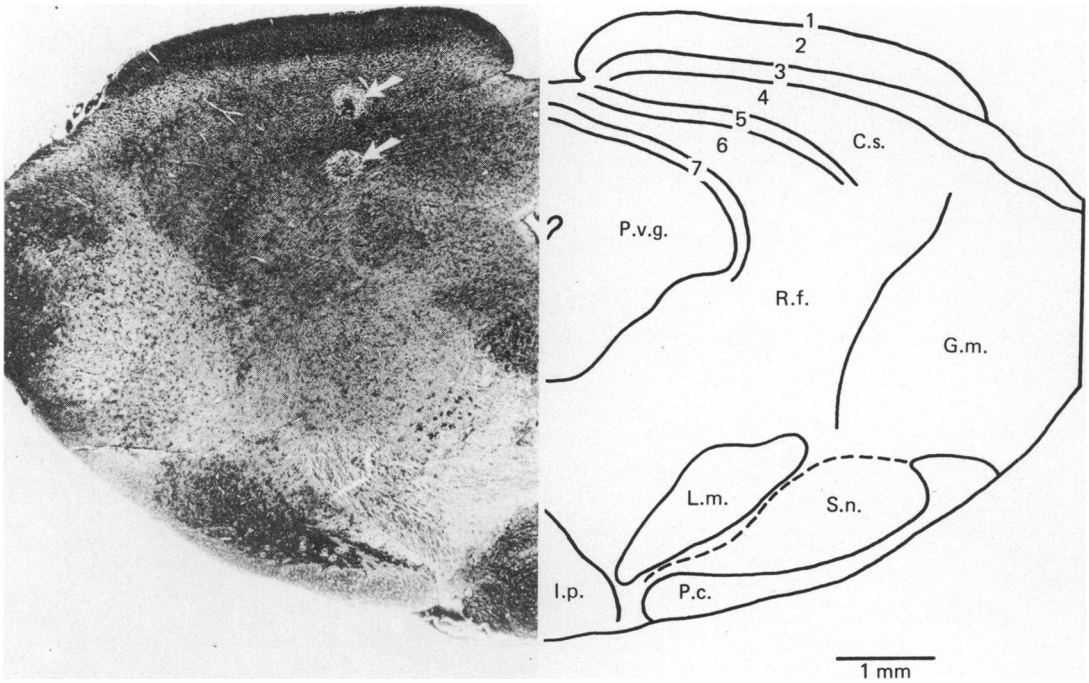
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EXPLANATION OF PLATE

Photomicrograph of a 15 $\mu$m paraffin section of the superior colliculus with an outline drawing of the other side on which is marked the laminae 1–7. The section was stained for fibres (Marsland *et al.* 1954) and counter stained with Cresyl Fast Violet for Nissl substance. The arrows mark the position of electrolytic lesions. C.s.: superior colliculus, G.m.: medial geniculate, I.p.: interpeduncular nucleus, L.m.: medial lemniscus, P.c.: cerebral peduncle, P.v.g.: periventricular grey, R.f.: reticular formation, S.n.: substantia nigra.